

Review

Mouthparts of flower-visiting insects

Harald W. Krenn*, John D. Plant, Nikolaus U. Szucsich

Institute of Zoology, University of Vienna, Althanstraße 14, 1090 Vienna, Austria

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Abstract

This review deals with the morphology and function of adult insect mouthparts modified to feed on nectar, pollen or petals. Specialization to nectar-feeding is evident in formation of proboscides of various lengths and designs. Proboscides of many Hymenoptera and Diptera function according to adhesion mechanisms that load nectar onto extensible apical mouthpart regions before fluid is conveyed along the food canal to the mouth by capillarity and suction. Predominantly suctorial proboscides evolved once in Lepidoptera, probably twice in Coleoptera, variously in some Hymenoptera and several times with similar design in Diptera. Many of them are particularly long and have sealed food tubes, specialized apical regions, new proboscis resting positions and modified feeding movements. Mouthparts of obligate pollen-feeding insects can be characterized by modified mandibles, specialized bristles for pollen manipulation and elaborate feeding movements. Often saliva is crucial for pollen retention and ingestion. In Coleoptera, intact pollen is gathered by sweeping movements of mouthparts; in Diptera, it is suspended in saliva prior to suction. Pollen is crushed by asymmetrical mandibles in aglossatan Lepidoptera and one group of basal Hymenoptera. Pollen-piercing mouthparts occur in Thysanoptera and one group of Diptera. Some butterflies and few Diptera extract nutrients from pollen by mixing it externally with saliva on their mouthparts. No mouthpart specializations to petal-feeding are reported in flower-visiting insects.

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1. Introduction

The majority of flower-visiting adult insects belongs to the bees, wasps, flies, butterflies, moths and certain beetles. They obtain nutrition from floral nectar and pollen and a few from petal tissue. Occasionally, adults from other orders (Table 1) also feed on floral food. In many instances they ensure the pollination of the plants they visit. In addition to food, flowers are frequented to collect fragrances, to seek shelter, prey, larval hosts and mates.

Insect–flower associations are multifaceted and can be examined from botanical, entomological, ecological or evolutionary viewpoints which are often summarized under the heading of pollination biology (e.g. Kevan and Baker, 1983; Paulus, 1988; Thompson, 1989; Heß, 1990; Proctor et al., 1996; Pellmyr, 2002; Lunau, 2004). Paleontological evidence indicates that the co-radiation of

major groups of specialized flower-visiting insects and angiosperms took place in the Cretaceous period (Grimaldi, 1999). This was preceded by evolution in the late Jurassic and early Cretaceous of angiosperm pollinating insects with generalized mouthparts (Labandeira, 1997, 2002). Adaptation to flower-visitation has led to behavioral and learning developments, elaborate sensory apparatuses (Barth, 1991; Lunau, 1996), increased flight abilities (Dudley, 2000) and morphological specialization of mouthparts. Comparative descriptions of various insect mouthparts are given in benchmark treatises of Weber (1933), Snodgrass (1935) and Matsuda (1965). Functional aspects of adult and larval mouthpart feeding are reviewed by Smith (1985) and Chaudonneret (1990). These works, however, do not focus on flower-visiting insects.

We review and attempt to synthesize current understanding of the form and functional mode of adult mouthparts in flower-visiting insects and to discuss aspects of convergent evolution to different floral foods regardless whether the insects achieve pollination or not.

* Corresponding author. Tel.: +43 1 4277 54497; fax: +43 1 4277 9544.
E-mail address: harald.krenn@univie.ac.at (H.W. Krenn).

Table 1
Insect orders which contain representatives that feed on flowers

Insect orders	Food sources and feeding behavior	References
Collembola	Facultative nectar and pollen-feeding	Porsch, 1957; Kevan and Baker, 1983
Plecoptera	Nectar-feeding rarely observed	Porsch, 1957
Dermaptera	Various floral tissues	Porsch, 1957
Blattodea	Flower visiting rarely observed	Porsch, 1957
Orthoptera	Anthers and petal-feeding	Porsch, 1957; Schuster, 1974
Mantodea	Supplementary pollen-feeding of nymphs in <i>Tenodera</i>	Beckman and Hurd, 2003
Hemiptera	Nectar-feeding in few Lygaeidae	Rammer, 1942; Porsch, 1957
Thysanoptera	Piercing sucking of pollen and floral tissue	Hagerup, 1950; Hagerup and Hagerup, 1953; Kirk, 1984; Williams et al., 2001
Coleoptera	Pollen, nectar and tissue-feeding	Fuchs, 1974; Kevan and Baker, 1983; Proctor et al., 1996
Neuroptera	Obligate pollen-feeding in <i>Nemoptera</i>	Porsch, 1957; Popov, 2002
Hymenoptera	Nectar and pollen-feeding widespread, some collect pollen as larval food. Occasional petal-feeding	Kevan and Baker, 1983; Hanson and Gauld, 1995; Proctor et al., 1996; Jervis, 1998; Jervis and Vilhelmsen, 2000
Trichoptera	Nectar-feeding uncertain	Ulmer, 1905
Lepidoptera	Mostly only nectar-feeding; pollen-feeding is plesiomorphic; derived in Heliconiini	Norris, 1936; Gilbert, 1972; Scoble, 1992; Kristensen, 2003
Mecoptera	Nectar-feeding rarely observed	Porsch, 1957
Diptera	Nectar and pollen-feeding in many taxa	Downes, 1958; Kevan and Baker, 1983; Gilbert and Jervis, 1998; Larson et al., 2001

Bold letters indicate those taxa which contain obligatory flower-visiting species. Most cited references give overviews for the respective taxa.

2. Nectar-feeding

Two principal mechanisms are deemed responsible for the uptake of surface liquids or nectar from flowers (Kingsolver and Daniel, 1995) which are not mutually exclusive: adhesion and suction. Mouthparts, which function in accordance with the properties of adhesion and capillarity possess a wettable apical surface and perform licking, lapping, dapping or sponging movements to draw fluids into the mouthparts. Mouthparts which function according to a purely suctorial mode often have greatly elongated and tubular food canals to take nectar from flowers with long and/or narrow corolla tubes. These mouthparts generally remain motionless during feeding and suck nectar along a pressure gradient according to the principle of a soda straw.

The most common resource utilized by flower-visiting insects is nectar secreted from floral glands. Nectar varies in sugar concentration from 5 to 75% and contains glucose, fructose and sucrose, as well as various amounts of amino acids and other substances (Baker and Baker, 1983; Kevan and Baker, 1983; Dafni, 1992; Proctor et al., 1996). Flowers can be broadly grouped according to floral architecture and degree of nectar accessibility into those offering only pollen, those with exposed nectaries, partially hidden nectaries (bowl-shaped flowers or under a flap of petal tissue) and nectaries concealed at the base of long, narrow, tubular corollas (e.g. Heß, 1990; Patt et al., 1997; Jervis and Vilhelmsen, 2000). Some of the most spectacular nectar-feeding mouthparts are those associated with deep flower-tubes (e.g. Nilsson, 1988; Johnson and Steiner, 1997). Various elongate suctorial proboscides have independently evolved in species of Coleoptera, in many lineages of Hymenoptera and Diptera and within the glossatan Lepidoptera. These mouthparts are

appropriately labeled ‘concealed nectar extracting apparatuses’ (Jervis, 1998; Gilbert and Jervis, 1998). In addition to these highly specialized obligatory nectar-feeding insects many others are known to feed occasionally on floral nectar with unspecialized orthopteroid or with piercing/sucking mouthparts (Table 1).

2.1. Coleoptera

Anthophilous beetles from various families consume nectar, many in addition to pollen, from open flowers (Proctor et al., 1996). Their unspecialized mouthparts normally are prognathous (Kevan and Baker, 1983) and only slightly modified from the orthopteroid composition having bristles on the mandibles and setose maxillary and labial structures. Scarabaeid beetles load nectar using sweeping movements of setose maxillary structures in a manner resembling pollen collection (Johnson and Nicolson, 2001).

Meloidae from several taxa possess elongated mouthparts that are adapted for feeding from flowers with concealed and partially concealed nectaries (Handschin, 1929; Schremmer, 1961; Kaszab, 1962; Chaudonneret, 1990). In *Lepipalpus* a proboscis is composed of the greatly elongated 4-segmented maxillary palps (Handschin, 1929). The distal segments are densely covered with short setae on their median sides. During feeding they are brought together to form a median food canal, which extends further than the head. Proximally, setae from labrum, galea, lacinia and labium join together on the posterior side to form a continuation of the food tube leading to the mouth. The tip of the proboscis bears an apical sensory pad and a subapical organ with bottle-shaped sensilla. In the resting position the proboscis is flexed at the base of the first

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